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# On Two Sacoglossan Slugs from Brazil

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The two species described in the present article live in patches of green algae on the surface of mud in mangrove. The first specimens were found in a sample collected by Dr. Sebastian A. Gerlach (Kiel, Germany) near Cananéia, about 200 kilometers southwest of Santos, state of São Paulo, Brazil. Later both species were found in the same biotope at São Vicente, near Santos, where much of the shore of the *"mar pequeno,"* the name given to the brackish broad mouth of the river Casqueiro, is covered by mangrove.

We express our thanks to Dr. Gerlach, also to Mme. Alice Pruvot-Fol (Sceaux), Dr. Vera Fretter (London), Dr. Kathleen White (Reading), and Messrs. Kikutaro Baba (Osaka), Hendrik Engel (Amsterdam), T. J. Evans (London), Siegfried Jaeckel, Jr. (Kiel), Henning Lemche (Copenhagen), Alexander Luther (Helsingfors), Charles H. O'Donoghue (Reading), and Erich Schulz (Kiel), who kindly sent us copies of their papers pertinent to our subject.

## *Stiliger (Stiliger) talis,* new species

Figures 1–7

This and the East African *S. irregularis* Eliot, 1904, are the smallest known species of *Stiliger*. The largest living slugs attain 2 mm. in length but a preserved specimen 0.8 mm. long was already mature. Transverse sections measure 0.45 mm. high and 0.48 mm. wide, with a sole 0.24 mm. broad, of which 0.18 mm. is ciliated.

The animals are transparent or white, with superficial purplish black

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pigment dorsally. Ciliated epidermal areas lack pigment. Pigment is wanting from the middle of the head, the rhinophores, the areas around the subepidermal black eyes, and the sole. The sides of the head and the cerata are slightly pigmented. The cerata contain white glands (fig. 3, m). The cerata are colored by the enclosed diverticula of the liver which are green from ingested algae; the green granules lie in the lumina and hepatic cells (fig. 5, h) and are lost in hungry slugs.

The anterior border of the head has a median notch flanked by slight bosses that lie beside the mouth and might represent vestigial tentacles. The rhinophores form smooth cylinders, not grooved. The foot is anteriorly broader than the head but medially and posteriorly narrower than the body. The fore end of the foot forms two rectangular lobes (fig. 2) separated by a median notch. There are inconspicuous sole glands (fig. 5, ai) and a rather short tail.

As a rule, the largest specimens have three cerata on each side, of which the second is the biggest. A primordium of a fourth ceras lies between the first and second. Only once were four fully developed cerata noted on one side of a specimen. The cerata are clavate, with round tips (fig. 3); one bifid ceras was seen. Unbranched diverticula of the liver enter the cerata (fig. 3), and rather voluminous unicellular glands (fig. 3, m) lie between the hepatic diverticulum and the epithelium at the end as well as on the sides of the cerata. Trinchese's musk glands (Hoffmann, 1932–1939, p. 412), the glands drawn and described by Bergh (1877, pl. 11, fig. 12; 1878, p. 819), and the glands in the cerata of *Hermaea coirala* (Marcus, 1955, p. 108) are identical with the glands of the present species, which occur also on the body, appearing white in living slugs. Two symmetrical pellets of secretion emerging from such glands in front of the rhinophores were seen in one preserved slug. Perhaps these glands are defensive. They are generally empty in sections.

The anus (fig. 3, a) opens on the dorsal surface, without a papilla, a little to the right, on a level between the first and second pairs of cerata. The renal aperture lies immediately beside the anal opening; the kidney is a flat sac. The pericardium is not externally visible. The male pore (fig. 6, t) of a sectioned animal 1.2 mm. long lies 0.3 mm. from the anterior end, slightly behind the level of the eyes. The orifices (fig. 6, u, v) of oviduct and vagina are located 0.36 and 0.54 mm., respectively, from the anterior border. All genital openings lie on the right side (fig. 6), about halfway between back and sole.

The glands of the buccal tube (fig. 3, b) open at different points but are not arranged in definite anterior and posterior groups. The fold between the buccal and pharyngeal cavities is cuticularized, thus forming a

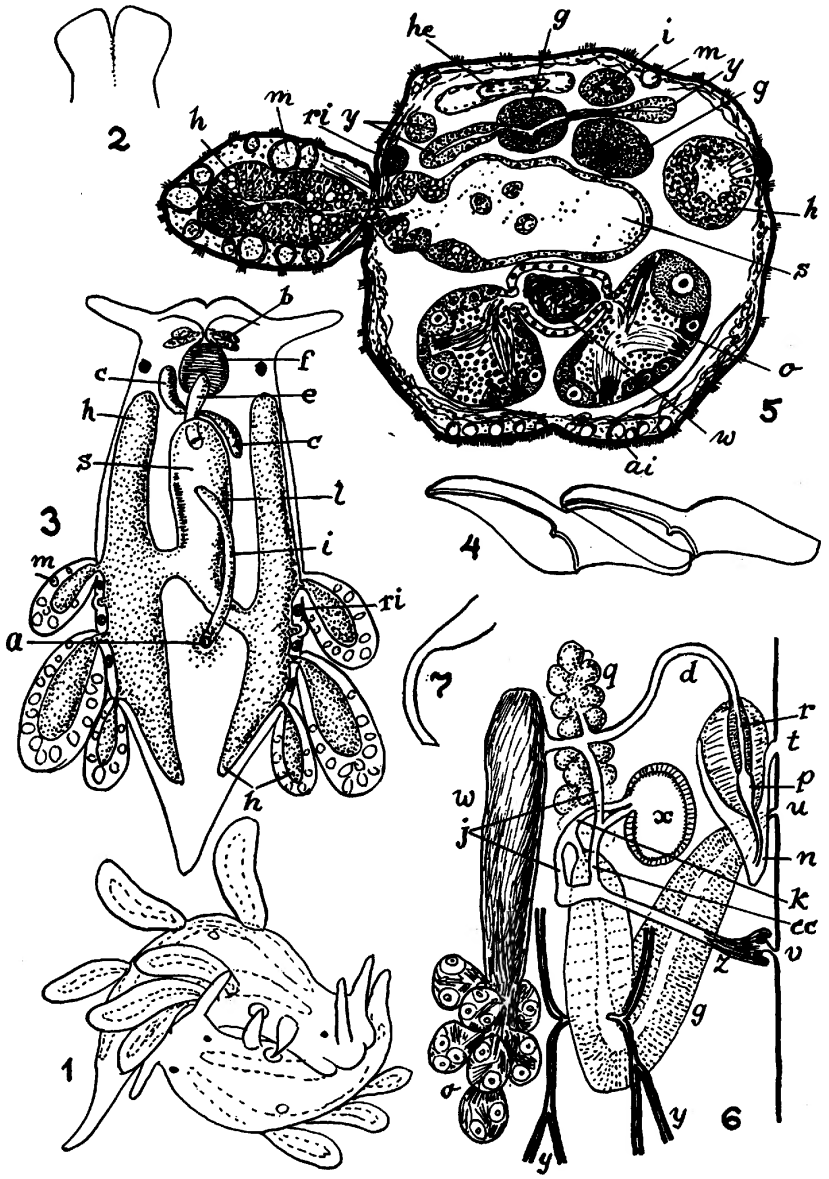
"labial disc" (Hoffmann, 1932–1939, p. 942). The salivary glands, with basophilous secretion, are long, thick-walled tubes (fig. 3, c) and reach the level of the heart which lies on the same level as the vaginal pore.

The radula (fig. 4) consists of five plates in the ascending limb, five in the descending limb, and four curled up in the ventrally prominent ascus. Base and shoe-shaped tooth with smooth borders are of equal length. The 0.1-mm. long esophagus (fig. 3, e) opens from the ventral side into the thin-walled stomach (s). The latter has no folds except a 0.1-mm. long ciliated ridge (1) on each side. The 0.1-mm. long slender gut (i) leaves the stomach on the dorsal side of the latter, shortly behind the entrance of the esophagus (fig. 3). Farther posteriorly the stomach continues into one hepatic duct on the right side and another on the left. The liver lobes (h) are wide tubes extending from behind the eyes to the tail, and give off as their only branches a smooth diverticulum into each ceras (fig. 3).

The mixed follicles of the ovotestis (fig. 5, o), seven to 10 in number, form one ventral layer in the posterior body half, whereas there are much more numerous and also dorsal acini in *S. bellula* (Bergh, 1872, p. 143; 1886, p. 14). Every follicle opens by a short duct into the sausage-shaped ampulla (fig. 6, w), 0.32 mm. long. The hermaphroditic duct leaves the side of the anterior part of the ampulla (fig. 6). Where it divides it communicates with the branched gland ("verzweigte Drüse") that is considered to be the prostate (fig. 6, q). The male duct (d) enters a 0.1 mm. long muscular penial bulb, where its epithelium (r) becomes tall and glandular. The duct ends with a slightly curved stylet (p), 60 micra long, mostly 7 micra in diameter, with an obliquely truncated tip.

The female branch (fig. 6, j) of the hermaphroditic duct enters the inner limb of the U-shaped mass (g) of the mucous gland. This limb stains pale blue, whereas the outer limb is intensely basophilous. Near the bend of the U there open into the mass the two ducts of the tubular albumen glands (y) which are of eosinophilous nature. They are somewhat ramified and accompany the hepatic tubes on the dorsal side but do not enter the cerata. The vagina (z) presents a small pouch just prior to its pore, and in a slug preserved immediately after mating this pouch contains spermatozoa with their heads fixed into its outer wall (fig. 6). The copulatory communication (cc) between vagina and spermatheca (x) functions also as an oviduct. The insemination duct (fig. 6, k) that corresponds to the uterine duct of the doridiids reaches the oviduct (j) near the entrance of the latter into the inner limb of the gland mass.

HOLOTYPE: One preserved specimen of *Stiliger talis* deposited in the invertebrate section of the American Museum of Natural History.




FIGS. 1–7. *Stiliger talis*. 1. Living slugs mating. 2. Fore end of foot. 3. Alimentary tract, reconstructed from sections. 4. Two plates of radula. 5. Transverse section through middle of body. 6. Reproductive organs. 7. Penial stylet. *Abbreviations:* a, anus; ai, sole glands; b, glands of the buccal tube; c, salivary glands; cc, copulatory path for sperm; d, efferent duct; e, esophagus; f, pharynx; g, mucous gland; h, liver; he, heart; i, intestine; j, oviduct; k, insemination path of sperm (uterine duct); l, ciliated ridge of stomach; m, cutaneous glands; n, male antrum or vestibule; o, ovotestis; p, penial stylet; q, prostate; r, glandular part of efferent duct; ri, regeneration cells for lost cerata; s, stomach; t, male pore; u, orifice of oviduct; v, aperture of vagina; w, ampulla; x, spermatheca; y, albumen glands; z, vagina.

## Notes on Occurrence and Biology of *Stiliger talis*

We obtained a total of 20 mature slugs from Cananéia and at São Vicente near Santos in patches of green algae, probably *Vaucheria,* entangled with mud among mangrove in the intertidal zone. Here *S. talis* lives in company with *Alderia uda* but was much less numerous than the latter in June and July, 1954. In September, 1954, the two species were present in about equal numbers at São Vicente. At this time the patches inhabited by the slugs were found covered with a thin layer of mud, hence no more specimens were obtainable from the algae, although this was still alive. About 5 meters away, however, both species were taken in uncovered algae exposed to light and air. The salinity of the localities varies but is always lower than that of the open sea. The egg mass of *S. talis* is similar to that of *Alderia uda* shown in figure 11, being about 2 mm. long, 0.6 mm. broad, curved in the middle, with rounded ends.

The cerata pulse slowly and change form continuously in living slugs. Respiratory and digestive movements of sacoglossan cerata are described in the literature (Hoffmann, 1940, pp. 65–66; Evans, 1953, p. 250). The cerata of the present species fall off easily on mechanical contact as with the surface film. A group of undifferentiated cells with big nuclei and richly staining cytoplasm occurs in the body cavity in relation to each ceras (fig. 3, ri) ; we suggest that these are reserve cells for the regeneration of the cerata. Davenport (1893, pp. 142–146) and Hecht (1895, p. 609) also found cells that they presumed to be regenerative material for cerata, but their descriptions and figures do not agree with our finding.

## Discussion of *Stiliger talis*

*Calliopaea fuscata* Gould, 1870 (p. 250), from Boston, the only *Stiliger* previously described from American coasts, is possibly identical with *talis,* although considerably longer (7.6 mm.), but the generalized nature of the original description, lacking even an account of the radula, makes it impossible to establish identity. *Stiliger fuscatus* (Gould) continues to be considered as a valid species in the North American literature (Johnson, 1934, p. 153; Russell, 1946, p. 96), but we have not seen any modern description. Although Russell obtained 12 specimens in the tide pools on the alga *Enteromorpha clathrata* in the vicinity of Woods Hole, he gave no description beyond the dimensions (1/4 inch long by 1/32 inch wide). It is strange that Bergh (1886, p. 11, note 1) separated *Stiliger fuscatus* (Gould) expressly from *Embletonia fuscata* Gould, 1870 (p. 251), but confounded them some pages later (1886, pp. 35, 37), when he examined material of *Embletonia fuscata* Gould that Verrill had sent him under this name.

It is probable but not beyond all doubt (Eliot, 1906a, p. 380) that *Stiliger ornatus* Ehrenberg, 1831, and *Calliopaea bellula* d'Orbigny, 1837, are congeneric. Despite several papers on the opisthobranchs from the Read Sea by Vayssière (1906, 1912), Eliot (1908), Pruvot-Fol (1933), and White (1951), Ehrenberg's *S. ornatus* (4.36 mm. long, alive) has not been refound. Alder and Hancock (1845–1855, pt. 7, appendix p. xxiii), Eliot (1906a, p. 380), O'Donoghue (1929, p. 738), and Pruvot-Fol (1933, p. 93) write the name correctly, *Stiliger ornatus* Ehrenberg, whereas Bergh's erroneous *Stiliger modestus* Ehrenberg (Bergh, 1872, p. 139; 1878, p. 812; 1886, p. 10) is repeated in Thiele's "Handbuch" (1931, p. 414).

Bergh obtained from Costa original material of *Embletonia viridis* and *E. nigrovittata* Costa, 1866 (p. 75, pl. 3, figs. 1–3) and gave descriptions and figures of them (Bergh, 1877, pl. 10, figs. 10–14, pl. 11, figs. 12–13, pl. 12, figs. 13–14; 1878, pp. 814–822, pl. 10, figs. 1–19, pl. 12, figs. 1–5; the explanations of the last two figures in the 1877 article, p. 764, must be interchanged). He reduced *E. nigrovittata* to a variety of *E. viridis* and transferred them to *Ercolania* Trinchese, 1872. Some years later Bergh (1886, p. 34, note 1) referred to them as seeming to be "Hermaeinen." This may be a lapse for "Ercolanien," but as both names are given specific rank, it appears that Bergh had forgotten his decision of 1878.

When Trinchese (1872, p. 87) separated *Ercolania* from *Stiliger* the genus *Calliopaea* had already been united with the latter (Alder and Hancock, 1845–1855, pt. 7, appendix p. xxiii) but Trinchese considered only *S. ornatus* Ehrenberg. Thus Trinchese's distinctive characters of *Ercolania* are more numerous than those retained by Bergh (1878, p. 813), viz., a posterior tubular prolongation of the pericardial prominence, and a groove or flattening (Pruvot-Fol, 1951, p. 70) on the outer side of the rhinophores. It is true that the latter character, the *"meplat"* of Pruvo-Fol, disappears in preserved slugs and individual variation of the rhinophore shape from auriculate to cylindrical occurs, at least in *Hermaea dendritica* Alder and Hancock (Pruvot-Fol, 1929, p. 530). *Calliopaea felina* Hutton, 1883, was placed in *Stiliger,* not *Ercolania,* by Eliot (1907, p. 330), although it has a bladder-like ridge directed backward from the prominent pericardium. It is therefore advisable to maintain *Stiliger, sensu stricto,* and *Ercolania* only as subgenera (Eliot, 1910, p. 177) or sections (Thiele, 1931, p. 414) of *Stiliger,* not as genera.

Vayssière (1888, pp. 122–125, pl. 6, figs. 103–106, pl. 7, figs. 112–113) identified material from Marseille with *Embletonia funerea* Costa, 1867, and gave a description recognizable as a true *Stiliger,* as previously supposed by Bergh (1886, p. 34, note 1). Nevertheless, Vayssière called the

species *Ercolania funerea* and indicated as synonyms three true *Ercolania,* namely, *viridis* (Costa), 1866, *nigrovittata* (Costa), 1866, and *siottii* Trinchese, 1872. Vayssière retained *funerea,* as *viridis* and *nigrovittata,* although described one year earlier, are juvenile forms. Except for the substitution of *funerea* by *viridis,* O'Donoghue (1929, p. 739) followed Vayssière (1888, 1913). O'Donoghue applied the generic name *Stiliger* to the five species he recorded from the Mediterranean and said that they belong to *Ercolania* if this genus is to be separated from *Stiliger.* However, *S. mariae* and *S. vesiculosus* of his list, as well as *S. funereus,* are true *Stiliger.*

As far as the literature is available the species of *Stiliger* are listed here and, in those of the subgenus *Stiliger,* one or more characters differentiating them from the present new species are given:

1. *Stiliger* (*Stiliger*) *ornatus* Ehrenberg, 1831, the description of which was copied by Trinchese (1872, p. 88). Eleven transverse rows of cerata, totalling 64; back dark green, sole yellowish; base and tip of rhinophores yellow, middle a blue ring; cerata with green base, dark blue middle, golden subapical zone, and black tip.
2. *Stiliger* (*Stiliger*) *bellula* (d'Orbigny, 1837, p. 12); spelling after White (1938, p. 19). Synonym: *Embletonia mariae* Meyer and Möbius, 1865 (p. 17; see Bergh, 1872, p. 139; 1886, p. 11; also Eliot, 1906a, p. 379; 1910, p. 177). Base of radula plate much shorter than cusp (see also Labbé, 1931, fig. 7); anterior angles of foot produced and pointed; stylet 10 times as long as in *talis.*
3. *Stiliger* (*Stiliger*) *souleyeti* (Verany, 1853, p. 385). As Souleyet's "Mollusques et zoophytes du voyage de la Bonite" (1852) is not available to us and Vernay's listing of the name (1853, p. 384) does not include morphological data, we must separate *souleyeti* from *talis* on the basis of Bergh's note (1872, p. 143, note 1): hepatic diverticula covered with numerous large knobs.
4. *Stiliger viridis* (Kelaart, 1859, p. 492). See also Eliot (1906b, p. 686). Very large (13 mm.); with 24 pointed cerata on the right side and 21 on the left; genus uncertain.
5. *Stiliger* (*Stiliger*) *vesiculosus* (Deshayes, 1839–1853, pl. 89, fig. 2, no text). See also Fischer (1871, p. 91) and Pruvot-Fol (1951, p. 72). Hepatic diverticula much branched in the swollen, nearly globular cerata.
6. *Stiliger* (*Ercolania*) *viridis* (Costa, 1866, p. 75). See also Bergh (1878, p. 814). According to Vayssière (1929) this species is identical with *S.* (*E.*) *pancerii* (Trinchese, 1872).
7. *Stiliger* (*Ercolania*) *nigrovittata* (Costa, 1866, p. 75). According to Bergh (1878, p. 821) this is a variety of *viridis,* and according to Vayssière (1929) this and *viridis* are identical with *Stiliger* (*Ercolania*) *pancerii.*
8. *Stiliger* (*Stiliger*) *funereus* (Costa, 1867, p. 36). See also Bergh (1886, pp. 11, 34, note 1); Vayssière (1888, p. 122; 1913, p. 231). Rhinophores one-third of the body length of 16 mm.; penial papilla five times as long as the stylet.
9. *Stiliger* (*Stiliger*) *fuscatus* (Gould, 1870, p. 250). More than three times as long as *talis.*

10. *Stiliger* (*Ercolania*) *pancerii* (Trinchese, 1872, p. 120). Given by Vayssière (1913, p. 232; 1929) as *Ercolania pancerii*.
11. *Stiliger* (*Ercolania*) *uziellii* (Trinchese, 1872, p. 121); Vayssière (1913, p. 232, pl. 25, fig. 1); O'Donoghue (1929, p. 739, name only).
12. *Stiliger* (*Ercolania*) *siottii* (Trinchese, 1872, p. 121). Vayssière (1929) mentions this species as a synonym of *S.* (*E.*) *pancerii*.
13. *Stiliger felinus* (Hutton, 1883, p. 118). According to Eliot (1907, p. 330) with a ridge directed backward from the pericardium; anal papilla to the left; foot not notched.
14. *Stiliger* (*Ercolania*) *zanzibaricus* (Eliot, 1903a, p. 256).
15. *Stiliger* (*Stiliger*) *varians* Eliot (1904, p. 291). Length, 10 mm.; brilliant green; 10 transverse rows of cerata, with four to five cerata on each side of a central space; three to four small hepatic branches in each ceras.
16. *Stiliger* (*Stiliger*) *irregularis* Eliot (1904, p. 291). Cerata in 10 transverse rows, the hindmost longest.
17. *Stiliger pica* Annandale (1922, p. 700). Numerous sharply pointed cerata with white tips; stylet minute.
18. *Stiliger* (*Stiliger*) *niger* Lemche (1935, p. 134). Anus below the first row of cerata.
19. *Stiliger* (*Stiliger*) *berghi* Baba (1937a, p. 222). With seven to nine alternating large and small cerata with a small one foremost.
20. *Stiliger* (*Stiliger*) *boodleae* Baba (1938, p. 7). Cerata tipped with brown and much more numerous than in *talis*, arranged in seven to eight transverse rows.
21. *Stiliger* (*Ercolania*) *smaragdinus* Baba (1949, pp. 32, 129).
22. *Stiliger* sp. Pruvot-Fol (1953, p. 43). Evidently a true *Stiliger* with numerous swollen and pointed cerata that cover the middle of the back.

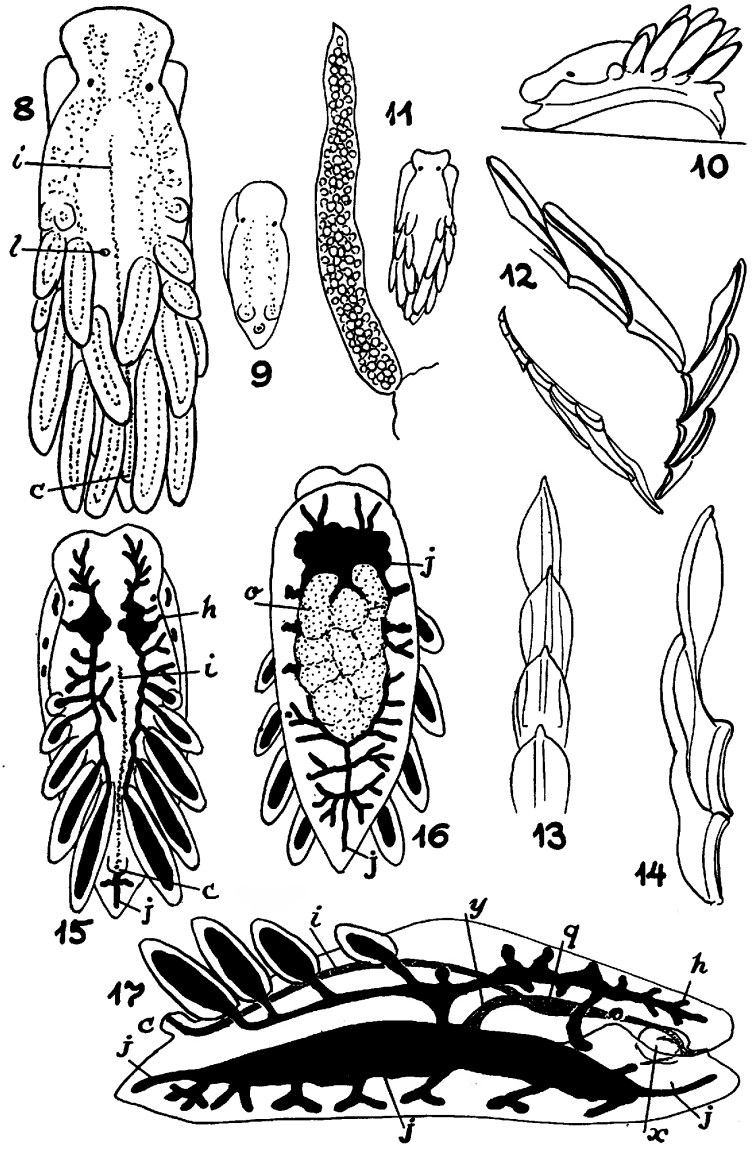
The descriptions of the following Indo-West Pacific species were not available to us, but it is highly improbable that any of them could be identical with *talis*: *Stiliger tentaculatus* Eliot (1917, pp. 179–182); *Stiliger (Ercolania) akkeshiensis* Baba (1935, pp. 115–116); *Stiliger gopalei* Rao (1937, pp. 435–451).

## *Alderia uda*, new species

Figures 8–23

Mature slugs (fig. 8) reach a maximum length of 4 mm., a breadth of 1.4 mm., and a height slightly less than the breadth. The cerata may attain a length of 1 to 1.5 mm. but are rarely so long. The smallest immature slugs (fig. 9) measured 0.6 mm. in length and 0.24 mm. in breadth. In the following description the measurements refer to a series of 170 transverse sections 10 micra thick of a slug that was 1.7 mm. long and indicate the distance from the anterior margin.

The animals are transparent, with a little black pigment dorsally, always less developed in the median line and in the cerata. Green color from the food shows in the midgut, stomach, liver, and cerata. The brown to




FIGS. 8–17. *Alderia uda*. 8. Adult living slug. 9. Smallest living slug. 10. Creeping slug. 11. Slug with spawn drawn to same scale. 12. Straight young radula. 13. Radula plates, surface view. 14. Radula plates, side view. 15. Dorsal view of slug, showing liver branches. 16. Ventral view, showing stomach. 17. Diagram of digestive apparatus. *Abbreviations:* c, anal papilla; h, liver; i, intestine; j, stomach; l, renal pore; o, ovotestis; q, esophagus; x, pharynx; y, cardia-pylorus part of stomach.

black contents of the intestine also show along the back. Black eyes, a generally white kidney, and the voluminous white glands of the cerata complete the colors.

The anterior end is a broadly rounded cephalic lobe medially notched and without appendages. The sides of the head are somewhat produced and in certain views appear triangular as in *A. harvardiensis* Gould, 1870 (pl. 16, fig. 227). They are, however, too inconspicuous to justify Gould's comparison with even short tentacles. Behind a constriction at the level of the eyes, the back widens towards the middle of the body. The cerata arise from the sides of the back, being absent from the anterior third or fourth. In large specimens there are up to 11 cerata on each side, disposed irregularly, without recognizable arrangement into longitudinal or transverse rows, contrary to the situation in *A. modesta* (Evans, 1953, p. 250; Rasmussen, 1951, fig. 19). The median caudal ones are the longest and form a median tuft. In young animals the knob-shaped first pair of cerata occurs near the posterior end (fig. 9).

The renal pore (fig. 8, 1), lying a little to the left at 0.87 mm., is very distinct in some living slugs. Its position near the body center differs from that of the nephroproct in *A. modesta* (Lovén), 1845, which is found in the anterior fifth or third (Engel, Geerts, and Altena, 1940, p. 19) or at the end of the second fifth (Evans, 1953, pl. 12). The conical anal papilla (fig. 8, c) lies 1.5 mm. from the anterior end. Behind it the dorsal side, separated from the foot by lateral furrows, ends in a pointed tail.

The foot is broader than the back, and its sharp margins are curved slightly upward in resting slugs. When gliding the animals often use only the broad and rounded anterior border of the sole.

As in *Stiliger talis,* cilia are borne only on the non-pigmented areas of the epidermis. The cilia form a broad middorsal stripe and cover not only the entire sole but also its lateral borders, approaching the lateral furrows. The dorsal epidermis and that of the cerata contain large glands like those described for *Stiliger talis,* mostly empty in sections as in the latter. The "strong sugar smell" of *A. modesta* (A. Hancock *in* Eliot, 1910, p. 137), probably produced by the secretion of the cutaneous glands, could not be verified in *A. uda;* we noticed a slight smell of carabids in a crushed slug. The sole lacks special glands.

The cerata vary in shape with state of contraction and may be cylindrical, clavate, or carrot-shaped, but never distinctly pointed. They contain a smooth liver diverticulum (figs. 15, 17, h), not branched as in *modesta,* and a voluminous blood sinus with a sphincter (see Hoffmann, 1940, p. 67, fig. 55b). Further blood lacunae, also with proper walls, occur in the rest of the body. Heart and pericardium are absent as in *A. modesta*

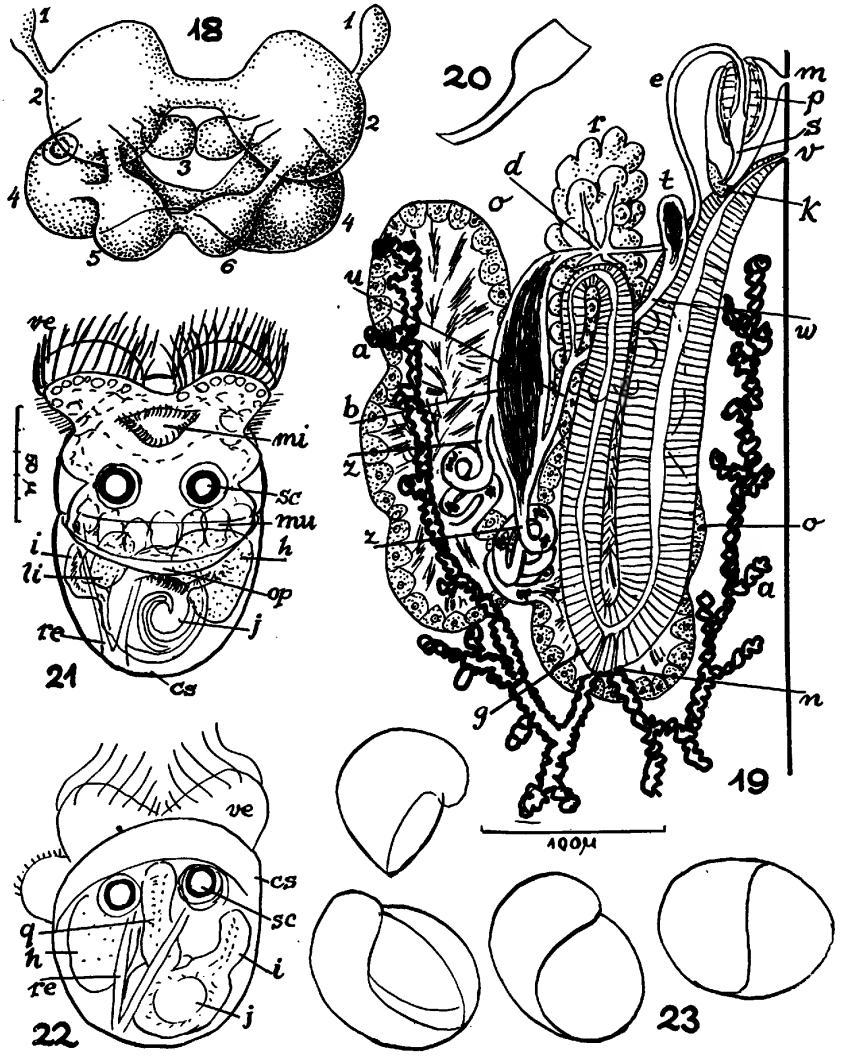
(Engel, Geerts, and Altena, 1940, p. 20; Evans, 1953, p. 251). In *A. uda* the kidney is a simple, flat, unbranched tube, beginning at 0.7 mm. from the anterior end and ending at 1.34 mm.; whereas in *A. modesta* the kidney opens more anteriorly and extends into the anal papilla with two blind canals. The body cavity of *A. uda* is rich in parenchymatous fibers as in *A. modesta* (Evans, 1953, p. 251).

The central nervous system (fig. 18) agrees with that of *Limapontia* as drawn by Hoffmann (1932–1939, p. 767, fig. 530D). The cerebral and pleural ganglia are coalesced (fig. 18, 2), the cerebral commissure is distinct, and there are two ganglia on the visceral loop—the large abdominal ganglion (fig. 18, 5) that perhaps includes the subintestinal ganglion, and the smaller supraintestinal ganglion (fig. 18, 6). Eliot's (1906a, pl. 11, fig. 30) figures of a median visceral (abdominal) ganglion connected with each of the pedal ganglia (fig. 18, 4) by a connective was already doubted by Hoffmann (1932–1939, p. 758); possibly Eliot in search of the third ganglion common in the visceral loop of the Sacoglossa thought the buccal ganglia to belong to the loop, although these are distinctly paired and separate from the loop (fig. 18, 3). Rhinophorial ganglia (fig. 18, 1) occur as in *Limapontia* (Hoffmann, 1932–1939, p. 760, footnote). Statocyst and statolith have the same diameter (18 and 14 micra, respectively) in the veliger and in a 1.2-mm. slug with already developed penial stylet.

The mouth is a perpendicular slit leading into the cuticularized buccal cavity that receives an anterior group of glands, staining light blue, and a posterior group, staining darker blue. No striation of the pharyngeal muscles was seen such as Fretter (1940, p. 192) described for *Hermaea dendritica*. The salivary glands are long tubes, reaching the level of the prostate, and are dilated into small ampullae near their openings into the pharynx.

The radula (fig. 12) comprises nine to 18 plates, up to six of which lie in the ascus. In young slugs the oldest plates form a straight row, whereas in the largest specimens they are parallel and tightly packed in the terminal widening of the ascus. The plates are smooth and shoe-shaped. The cusp is twice as long as the base; for example, a plate 85 micra long has a base 28 micra in length. A cusp is not recognizable in the smallest, oldest plates.

The narrow ciliated esophagus (fig. 17, q) leaves the pharynx (x) dorsally, and behind the nervous collar enlarges into a dilatation that contains many longitudinal folds and gives origin to two branches of the digestive tract (fig. 17). Of these the dorsomedian one is the intestine (i), a ciliated smooth canal that continues in the middorsal position to the anal papilla (c); the other (y) with folded lining curves downward at




FIGS. 18–23. *Alderia uda*. 18. Central nervous system, reconstructed from sections. 19. Reconstruction of reproductive organs. 20. Penial stylet. 21. Veliger, frontal view. 22. Veliger, from behind. 23. Empty larval shells. *Abbreviations:* a, albumen gland; b, ampulla; cs, shell of veliger; d, openings of prostate; e, efferent duct; g, mucous gland; h, liver; i, intestine; j, stomach; k, cushion in male antrum; li, kidney of veliger; m, male pore; mi, mouth of veliger; mu, mucous cells in foot of veliger; n, opening of albumen glands; o, ovotestis; op, operculum; p, penis; q, esophagus; r, prostate; re, retractor muscle; s, stylet; sc, statocyst; t, spermatheca; u, oviduct; v, female pore; ve, velum; w, spermathecal canal; z, hermaphroditic duct; 1, rhinophorial ganglion; 2, cerebropleural ganglion; 3, buccal ganglion; 4, pedal ganglion with statocyst; 5, abdominal ganglion; 6, supraintestinal ganglion.

0.55 mm. and enters the stomach (j), where the folds gradually flatten. No cilia are seen in sections (Fretter, 1940, p. 190). The stomach epithelium is, as in other Sacoglossa, indistinguishable from that of the liver (Hoffmann, 1932–1939, p. 1137). There are large balls of chloroplasts in the stomach cavity as well as in the lumina of the hepatic diverticula (Evans, 1953, p. 257) and green globules in the cells of both. The stomach (fig. 17, j) is extremely elongated, not spherical or transverse as in the Sacoglossa examined by Fretter (1940), and extends posteriorly nearly to the caudal end of the body. It sends two caeca to the ventral side of the pharynx. Anteriorly the stomach is broad and lies close to the ventral surface, medially it is elevated by the underlying ovotestis (fig. 16, o), and posteriorly it again approaches the sole. Lateroventral, often branched, stomach diverticula, the pedal digestive diverticula (Evans, 1953, p. 256, fig. 5), fill the lateral borders of the foot and attain greatest ramification in the tail. The connection of the stomach (fig. 17, y) with the esophagus and intestine is located dorsomedially. Dorsolaterally, at different transverse levels, the stomach communicates with the two lateral hepatic trunks, the *"Seitengänge"* and *"Seitenstämme"* of Hoffmann (1932–1939) or the lateral digestive diverticula of Evans (1953). From these trunks arise the unbranched liver diverticula into the cerata as well as the ramified tubules to the margins of the dorsal side (fig. 15). Behind the eyes the lateral hepatic trunks are dilated (fig. 15). The hepatic system of our species agrees with that of *A. modesta* (Eliot, 1906a, p. 378; 1910, pp. 138–139; Evans, 1953, pp. 254–256, figs. 5–6).

The voluminous confluent follicles of the hermaphroditic gland (figs. 16, 19, o) or ovotestis contain male and female germ cells in the same acinus; the ovocytes lie mostly peripherally, the male stages more centrally (fig. 19). The follicles lie ventrally and laterally to the stomach. From the ovotestis arise two thick and coiled hermaphroditic ducts (fig. 19, z) that are pigmented and ciliated. One duct dilates at 0.84 mm. and forms the ampulla (fig. 19, b), and the other enters the side of the ampulla at 0.72 mm. The male and female ducts leave the ampulla separately. The male duct (fig. 19, e) originates by the narrowing of the ampulla at about 0.55 mm., at first runs transversely, receiving the outlets (d) of the lobulate prostate (r), and then continues anteriorly as a thin and muscular canal. At 0.23 mm. it curves backward and enters the penial papilla (p) that projects into the male antrum and is 0.2 mm. long with a breadth of 90 micra at its root. The posterior wall of the male antrum bears a cushion of tall cells (k). The obliquely truncate stylet (s) is similar to that of *A. modesta* (Alder and Hancock, 1845–1855, pt. 5, pl. 43, fig. 19); it is 60–70 micra long, about 20 micra in diameter proximally, 7 micra distally. The male pore (m) lies at 0.24 mm.

The female duct leaves the proximal part of the ampulla at 0.77 mm. as a narrow ciliated oviduct (fig. 19, u) that enters the mucous gland (g) at 0.64 mm. At this entry a long and narrow canal (w) leads to the spermatheca (t), a bulbous enlargement extending anteriorly to 0.42 mm. The mucous gland is a simple tube that proceeds forward to 0.54 mm., then bends backward to a second curve where at 1.08 mm. it receives the two albumen or tubular glands (a). These are tortuous tubules that extend between the levels of 0.53 and 1.51 mm. They surround the liver, especially the posterior ends of the two hepatic trunks, and their tubules may enter some of the cerata. Distal to the entrance of the albumen glands, the mucous gland, now called common female gland, ascends anteriorly as a thick limb that opens on the right side by the female pore (v) located at 0.37 mm.

This slug is protandrous; only male germ cells are in lively development in specimens of 1-mm. length (preserved).

HOLOTYPE: One preserved specimen of *Alderia uda* deposited in the American Museum of Natural History.

## NOTES ON THE OCCURRENCE AND BIOLOGY OF *Alderia uda*

The first four specimens were brought to us by Dr. Gerlach in mud with algae from the mangrove zone in a lagoon at Cananéia. Later we found as many specimens as we wanted near Santos (São Vicente) in the same biotope. The water is brackish at both localities and of very variable salinity. When the tide runs out the mud is uncovered and that at São Vicente is fully exposed to the sun. A layer of mud with algae no more than 8 mm. thick contained many slugs. The algae, probably *Vaucheria,* form greenish patches on the mud and serve as food for the animals. When low water at 11 to 15 hours coincides with calm and sunny weather, the layer in which the slugs live is warmed to 30° C. or more, even in the winter months (June, July) of our observations. The site at São Vicente does not dry, for it is only a few meters from low-water line; we were able to reach the region where the animals live by way of a drain pipe through the soft mud.

The slugs survived for some weeks in laboratory dishes and laid eggs. The algae must be kept merely moist, not wet, because when under water iron bacteria overgrew them and killed them; hence the slugs starved. In the starved state they were yellowish gray like the dead specimen figured by Alder and Hancock (1845–1855, pt. 6, pl. 41, fig. 2).

The slugs shun the light, although they do not strictly avoid diffuse daylight. In a watch glass they frequently glide away from the side facing the window and creep out of the water on the opposite side. If a lamp is

used, the resting animals begin to move and dig down into the mud.

*Alderia modesta* is known to contract the cerata of the two sides alternately (Schulz, 1936; Friedrich, 1937; and others). A beating movement was sometimes observed in the anterior region of the back by Engel, Geerts, and Altena (1940, p. 23). In *A. uda,* however, contraction and swelling involve the entire body, including the cephalic lobe that contains the cephalic sinus (Evans, 1953, p. 251). Pulsation proceeds alternately on both sides, but the intervals between beatings are rather irregular. At 17° C., 16 to 32 pulsations per minute were counted in slugs at rest; within the same minute, contractions might vary from four to eight in 15 seconds.

Mating and spawning of our animals took place at night; we found the fresh spawn in the morning fastened to the highest points of the mud or to the glass. Generally two egg masses lie close together; they are simple, straight or bent tubes attached at the wider end and narrowing to the pointed free end (fig. 11). Their length varies from 3 to 7 mm., but is commonly 5 mm.; the diameter is 0.8 to 1 mm. There are 40 to 50 eggs in each millimeter of the mass, which hence comprises 250 to 300 eggs. The eggs are light yellow at first but turn white after a day or two.

The egg mass (nidosome of the O'Donoghues, 1922, p. 132) of *Alderia modesta* was described and figured by Alder and Hancock (1845–1855, pt. 6, pl. 41, figs. 4–5) and Engel, Geerts, and Altena (1940, p. 17, pl. 2). Schulz's description (1936, p. 43) is consistent with these. The shape of the egg mass varies with its length (Rasmussen, 1951, p. 236), and the three first-named references give the mass as containing a great number of small eggs, in transverse rows of two or three. Different from these is the drawing of Rasmussen (1951, fig. 20) which corresponds roughly to our material (fig. 11) and shows a simple egg string like a chain of beads with the eggs in single file. The numbers and measurements of the eggs agree also in Rasmussen's and our material. In the nidosome of *A. uda* the material connecting the eggs was only exceptionally recognizable, as the matrix is so delicate that the eggs appear like marbles in a sac.

The diameter of the egg capsule is 0.12 to 0.20 mm. in the present species; that of the egg or embryo 0.12 mm. A newly spawned nidosome contained at 9 A.M. 50 unsegmented eggs in the pointed end, more proximally 15 eggs in the two-cell stage, then 16 in the three- to four-cell stage, and the numerous remaining eggs in the broader end were in more advanced stages, up to gastrulation. The two first blastomeres are somewhat, but not very, unequal. From an egg mass deposited in the night of July 16–17 the veligers hatched on July 21, at an average temperature of 18° C. The embryonic development of *A. modesta* requires about the same period, five days, in the summer of northern Germany (Schulz, 1936, p.

44). In Amsterdam in October the first veliger of this species hatched after eight days (Engel, Geerts, and Altena, 1940, p. 26) or even much later (*ibid.*, p. 27). Rasmussen (1951, pp. 237–238) quotes these and further data for *A. modesta.*

The shell of the veliger is 90–120 micra long and 75–90 micra wide in *A. uda* (fig. 23), whereas in *A. modesta* (Rasmussen, 1951, p. 239) the veliger shell is 130 micra long, and even larger dimensions are shown in Schulz's figures (1936, figs. 1–2). The veligers of the two species are equal in size (0.15 mm. in length). The retractor muscle of the velum has a simple origin in *A. modesta* (Schulz, 1936, p. 46, fig. 3), whereas the muscle divides immediately into two bundles in *A. uda* (fig. 21, re). After swimming about for two days our larvae shed their shells, but as they did not metamorphose we do not know if the time of shell loss is normal.

## Discussion of *Alderia uda*

Our species is closely related to but not identical with *A. modesta* (Lovén, 1844), which is very well known from the studies of Engel, Geerts, and Altena (1940), Rasmussen (1951), Evans (1953), and other references cited in these articles. Further localities of its occurrence in the Netherlands were published by Hartog and Swennen (1952). Jaeckel (1952a, 1952b) summarized the ecology and distribution in the North and Baltic Seas.

*Alderia modesta* is more than three times as long as *A. uda;* its cerata are disposed in rows (Evans, 1953, p. 250) and contain lobulate hepatic diverticula; the terminal sac of its ascus contains loose, irregularly disposed teeth; its kidney has two posterior diverticula; and the renal pore is more anterior.

*Alderia nigra* Baba (1937b) has distinct tentacles and its cerata are arranged in a single row along each side of the broad, smooth, black back. Eliot (1910, p. 157) and Vayssière (1913, p. 232) afford accessible information about *A. comosa* Costa, 1866, from Naples. This species is said to be 8 mm. long, green, with numerous long cerata and with the anal papilla located behind the pericardium. Possibly Costa and Baba mistook the dorsal renal pore for the anal opening; otherwise their species do not belong to *Alderia.* "Numerous long cerata" as described for *A. comosa* is the only available character for distinguishing this Mediterranean species from *A. uda.*

It is difficult to differentiate clearly *Alderia uda* from *A. harvardiensis* Gould, 1870 (p. 254). The triangular lateral prolongations of the head "capable of considerable extension so as to resemble short tentacles" and

the foot twice as broad as the body differ only in degree from comparable features of *A. uda*. Gould's description and figures of the disposition of the cerata are discrepant (Eliot, 1910, pp. 137, 177), hence *harvardiensis* cannot be regarded as adequately defined, although its name seems to be currently applied to an *Alderia* of the northeastern coast of the United States (Johnson, 1934, p. 153). The cerata of *harvardiensis* are short and widen towards the tip and, as Gould emphasized (p. 255), do not increase in length towards the tail. These details must, for want of better characters, separate *harvardiensis* and *uda*.

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